

Phylogenetic systematics and zoogeography of Australian nudibranchs

2. Description of a new species of *Thecacera* with comments on the genus and its contained species

by
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ABSTRACT

Thecacera boyla n.sp is described from coastal northern Queensland. Its most striking character is the elaboration of the rhinophoral sheaths into long, mobile "tentacles" that serve as sensory appendages, apparently in lieu of velar papillae. The genus *Thecacera* is holophyletic and probably derived from *Polycera* - like polycerids. Because four (possibly five) of the six valid biological species are tropical, it is probable *Thecacera* is tropically centered. There appears to be a gradient of decreasing species diversity eastwards from southeastern Africa.

INTRODUCTION

Thecacera is one of the most distinctive genera in the Polyceridae because of its smooth and high body that lacks a pallial ridge, expanded anterior foot corners, truncated head without either velar processes or oral tentacles, pair of deep pre-rhinophoral pits, clavate and lamellate rhinophores that are non-retractile and surrounded laterally by large sheaths, three or five tripinnate gills that are non-retractile, pair of ceratiform post-branchial processes, integumentary spicules, large wing-like jaws, short and narrow radula with formula 2-6.2.0.2.2-6, projection at base of the shaft on lateral teeth, vas deferens with enlarged prostatic section, and armed penis.

The genus is well known to me by way of *Thecacera pennigera* Montagu, the first nudibranch I studied (Willan, 1976). The distinctiveness of the new species described here plus its significance for the definition of the genus merit its description in this series of papers on Australian nudibranchs. Four specimens of this new species are known to me, but I was able to study only one of them (the holotype) alive.

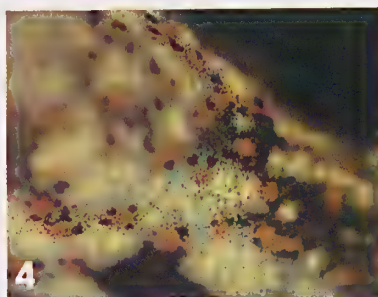
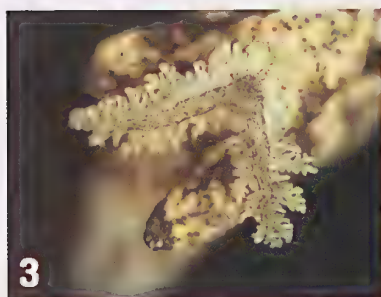
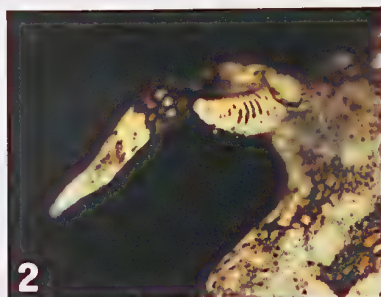
FAMILY POLYKERIDAE ALDER & HANCOCK, 1845
GENUS *Thekeria* FLEMING, 1928
***Thekeria boyla*, new species (Figs 1-13)**

Description

Thekeria boyla is a small, agile polycerid. When crawling in the fully extended state (Figs 1-5), the holotype measured 15 mm from head to tail. The body is elongate, high, rounded without any indication of a pallial ridge, and completely smooth. The body is highest and widest immediately in front of the gills where the pericardium is located. Minute, glassy, subepidermal spicules (Figs 14,15) are present all over the body; with the SEM they are seen to resemble the acanthostrongyle type of sponge megasclere. Dorsally, the foot is delimited from the mantle by an incised line. When *T. boyla* is crawling, its foot is narrower than the body except for the hind quarter which exceeds the tapering mantle in width. The posterior section of the mantle behind the gills has a distinct dorsal keel. When removed from a substrate, the foot margins come together in the ventral midline. The anterior corners of the foot are enlarged into dorso-ventrally flattened, triangular propodial tentacles and the mucous gland groove along the foot's anterior border is conspicuous. *T. boyla* leaves behind it a clear mucous trail. The mouth lies on the undersurface of the blunt head.

A deep pit with a semicircular orifice is present on top of the head immediately in front of each rhinophore. The anterior wall of this pit is overhung by an upward, and slightly outward, projecting lip. Internally, five, parallel, vertical ridges originate on the lip and descend down this wall into the pit. The orifice of the pit is dilated when the animal is at rest. The rhinophores have separate basal stalk and apical clavus sections (i.e., they are clavate). The clavus is erect and tilted slightly backward, and it possesses 16 oblique lamellae. Each rhinophore is guarded by a remarkable, incomplete sheath on the outer side (Fig. 2). The anterior margin of this sheath, which is low and broadly rounded, curves in front of the rhinophore. Medially the sheath is laterally compressed towards its base and its margin is steeply ascending. Posteriorly the sheath is drawn out into an enormous, tapering, pointed, flexible "tentacle" that is circular in cross section. When expanded the "tentacle" is approximately equal to half the body's length. The "tentacles" are extremely mobile, and during locomotion they are rapidly bent forward to touch the ground in front of the head and whipped upright again. These waving movements were very regular and it was possible to count an average of 20 per minute when the holotype was crawling actively. Usually both "tentacles" are waved at the same time, but each is capable of independent movement (as depicted in Fig. 5). When touched, these "tentacles" contract and come to lie alongside the body pointing backwards. However, they are rapidly returned to their upright position when the stimulus is removed. Because they are never "bristled" (i.e., held erect and/or waved provocatively) when the head or gills are touched, these "tentacles" apparently do not function as defensive organs like the nematocyst-loaded cerata of aeolid nudibranchs. These "tentacles" remain motionless when *T. boyla* is resting, and during quiescence they arch backward so that their tips almost touch the extremities of the lateral gills. The holotype had lost the tip of its right "tentacle". Each rhinophoral sheath has a vertical groove extending up the middle of its inner face. The genital aperture is located immediately behind the right rhinophoral sheath, approximately midway down the side of the body.

T. boyla has three, relatively small gills (Fig. 3). When fully expanded, the gills spread widely and radiate horizontally, the median one (which is shorter than the



Figures 1-4: Colour photographs of *Thecacera boyla* **holotype**, length 15 mm. 1, whole specimen from the left; 2, detail of left rhinophore and tentacle-like sheath; 3, detail of gills and post-branchial processes; 4, detail of body pigmentation.



Figures 5-9: *Thecacera boyla* holotype. 5, sketch of whole specimen from the right, based on a colour photograph of the living animal; 6, central nervous system (minus buccal ganglion) from the rear. Abbreviations: c-pl. = cerebropleural complex; p.c. = pedal commissure; p.e. = pedal ganglion; rh. = rhinophoral nerve; vi. = visceral ganglion; 7, single (6th) row of radular teeth; 8, entire jaws laid flat showing inner faces; 9, diagrammatic view of structure of untraveller reproductive organs. Abbreviations: alb. = albumen gland; amp. = ampulla; b.c. = bursa copulatrix; b.w. = cut body wall; d.v.d. = distal vas deferens; g.ap. = genital aperture; mu. = mucus gland; ov. = oviduct; p.sh. = penial sheath; pr. = prostate gland; p.v.d. = proximal vas deferens; r.s. = receptaculum seminis; v. = vagina.

lateral ones) pointing anteriorly and the lateral ones postero-laterally. Each gill is tripinnate with the smooth, rounded rachis raised and prominent above and the pinnae suspended below. The extra-branchial processes are bulky, flattened and triangular with a broadly rounded apex. Their length is approximately equal to that of the lateral gills. Each process has a groove extending one-third of the way up the centre of its inner face. The apical section of the left extra-branchial process had been damaged or lost in the holotype.

T. boyla appears slatey black and white mottled when viewed without magnification. However, its coloration and pattern are, in fact, most elaborate (Figs 1, 4). The translucent white body is marked with extensive, irregular black and creamish yellow non-overlapping patches that have imprecise boundaries. The black pigmentation is concentrated on the head, flanks, rhinophoral sheaths and extra-branchial processes. In addition, the body has superficial spots everywhere—larger, rounded, golden ones and tiny, intense black ones (Fig. 4). The genital aperture is ringed with gold. The foot sole is translucent white with grey-black speckling, and the propodial tentacles have some black spots but no black patches. The rhinophoral lamellae (Fig. 2) are decorated with cream patches, gold spots, and black streaks on their exposed faces. There is a black streak on the posterior face of the clavus. The anterior margin of the rhinophoral sheath is creamish white with a black margin. The proximal two-thirds (i.e., base plus "tentacle") of the sheath is black with gold and cream spots, and black specks. The gills (Fig. 3) are transparent; their raches as well as those of the pinnae are pale grey with scattered gold spots.

After fixation and preservation in 5% neutral formalin, the holotype's body shrank to 8 mm long by 4.5 mm maximum height. The "tentacles" contracted to just twice the height of the rhinophores, and the post-branchial processes swelled so that the groove on their inner faces could not be discerned. The colours faded to creamish grey with faint yellow spots; the black and cream patches as well as the intense black specks were unrecognizable. Numerous white spherules, invisible in life, could be seen in the integument all over the body except on the gills. Long preserved specimens are transparent white with an aggregation of orange spherules (?glands) at the apex of both post-branchial processes.

The central nervous system (Fig. 6) consists of a ring of ganglia concentrated around the oesophagus behind the muscular pharyngeal bulb. The ganglia of the cerebropleural complex are slightly larger, the cerebrals touching each other and delimited by a groove from the pleurals. There is a distinct swelling at the base of the rhinophorals, the largest of all the nerves emanating from the central nervous system. The eyes are sessile on the postero-dorsal face of the cerebrals. The pedal ganglia are separate and the commissure joining them is broader than the visceral commissure which it parallels ventrally. The visceral loop possesses, besides the visceral ganglion that almost touches the right pleural, two additional small swellings below the oesophagus.

The oral tube is large and wide (approximately the same diameter as the pharyngeal bulb) with a longitudinally-folded inner wall. The pharyngeal bulb itself is almost spherical with a short radular sac at the rear.

The radula (Figs 7, 10-13) is short and broad with a formula of $10 \times 2.2.0.2.2.$ Both laterals (Figs 12, 13) are relatively large, narrow, tall, and markedly recurved with a broadly rounded cusp. The shaft of both teeth possesses a projection on its outer margin; that arising from the larger outer lateral (Fig. 12) being substantially

stronger. Maximum vertical heights of the lateral teeth are $145\mu\text{m}$ and $170\mu\text{m}$ respectively. The inner marginal (Figs 10, 12) is a large, irregular plate lying flat against the basement membrane. It is broader anteriorly and it tapers to a thin, rounded extremity posteriorly. The outer marginal (Fig. 10) is very small, about $1/3$ the length of the inner marginal on whose antero-lateral corner it is situated, and merely an oval thickening on the basement membrane. Maximum vertical heights of the marginal teeth are $100\mu\text{m}$ and $40\mu\text{m}$ respectively.

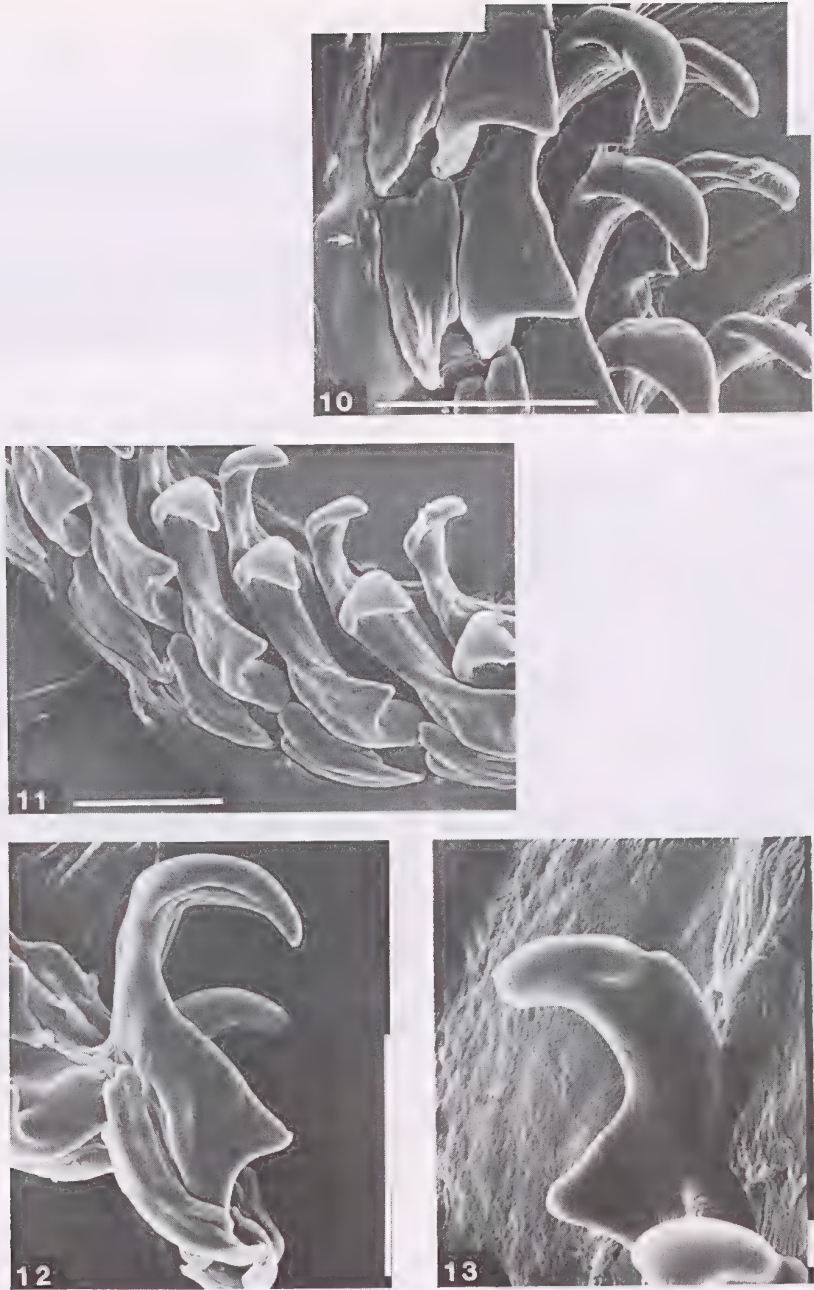
A pair of thick, cuticularized jaws (Fig. 8) lines the pharyngeal bulb. Each jaw has a curved, wing-like expansion arising from the centre of the tough masticatory border. The jaws are not quite symmetrical, the right having a more broadly rounded outer margin to its wing. Maximum length of the masticatory border is 0.45 mm and total height is 0.6 mm , of which the wing alone accounts for 0.5 mm .

A thin, transparent white tissue envelope surrounds the viscera. The large stomach is situated at the middle of the left postero-lateral face of the elongate, holohepatic digestive gland. The intestine runs forward along the left side of the digestive gland, across the anterior side, then backward along the right side until near the rear it shifts, as the short rectum, mid-dorsally to open at the anus.

A composite view of the reproductive system is shown in Figure 9. The ovotestis, which consists of a sheet of numerous closely compacted (but never more than one layer thick) creamish-white spherules, covers the digestive gland everywhere except on the left side where the stomach is located. The hermaphroditic duct is short, narrow and very thin walled. Its ampulla is kidney-shaped and creamish orange in colour. The hermaphrodite duct passes a short distance from the ampulla and then bifurcates. The narrower branch, the proximal vas deferens, passes rapidly into a large, white, spongy prostate gland that completely ensheaths the dorsal and anterior faces of the bursa copulatrix. This gland is flattened and so closely applied to the bursa that its removal intact was impossible. The prostatic section gradually narrows into a long distal vas deferens which maintains its diameter before expanding terminally as the penial sheath. The penis (Fig. 16) is an elongate rod covered with numerous, narrow, parallel-sided spines (Fig. 17) that are not aligned in rows. Maximum vertical height of a penial spine is $20\mu\text{m}$. The wider branch leading from the post-ampullar hermaphroditic duct, the oviduct, was difficult to trace. Its walls are thin and no ridges could be discerned internally; towards its mid-length is a swelling (a putative fertilization chamber). Its duct to the nidamental glands is minute. Two glands can be distinguished within the nidamental gland mass; a large, transparent mucous gland and a smaller, compact, solid and convoluted, opaque white albumen gland. Two allosperm receptacles (= exogenous sperm sacs) arise from the distal vagina immediately prior to its connection with the oviduct. The bursa copulatrix is larger, thin-walled and spherical; it contained a solid, brownish mass indicative of post-copulatory gametic remnants. The receptaculum seminis is smaller (approximately one-quarter the diameter of the bursa), club shaped, and it too has thin walls. There was no indication of an accessory receptaculum seminis.

Material

The holotype (Figs 1-17) was found on the undersurface of a small boulder at extreme low water spring level on the rocky headland at the S.E. end of Rows Bay, just N.W. of Townsville City, Cleveland Bay, northern Queensland, Australia, by Mr J. Brodie on 6 August 1988. Its dissected body is in The Australian Museum, Sydney, under the registration number C256696.



Figures 10-13: SEM's showing radular structure of *Thecacera boyla* holotype. 10, rows 3 (at bottom) 5, left half, tilted to show outer marginal tooth (arrowed) and outer faces of lateral teeth; 11, same 3 rows, seen in dorsal view; 12, isolated inner marginal tooth and outer lateral tooth from outer face, row 1, left half; 13, isolated inner lateral from inner face, row 10, left half. Bars (in Figs 10, 11 and 12) = 0.1 mm and (in Fig. 13) = 10 μ m.



Figures 14-17: SEM's showing integumentary and reproductive structures of *Thecacera boyla* holotype. 14, 15, isolated subepidermal spicules; 16, right profile of penis extended from penial sheath; 17, detail of penial spines. Bars (in Figs 14-16) = 0.1 mm and (in Fig. 17) = 10 μ m.

Three additional specimens from the collection of The Australian Museum were also examined: 1 specimen (5 mm preserved length), The Strand, Townsville City, Cleveland Bay, northern Queensland, Australia, I. Loch, May 1975, registration number C100530; 2 specimens (9, 4.5 mm preserved length) (plus colour slide of larger animal alive), under rocks at low tide, The Strand, Townsville City, Cleveland Bay, northern Queensland, Australia, I. Loch, 3 June 1975, registration number C100018.

Etymology

The specific name *boyla* is an Australian Aboriginal word for sorcerer (Reed, 1982). It is coined because of this nudibranch's coloration and behaviour of waving its enormous "tentacles" like a sorcerer's wand as it moves.

Remarks

The "tentacles" are the first feature of *Thecacera boyla* one notices; they dwarf the rhinophores. These distinctive, mobile structures distinguish this new species from all the other described species in the genus. None of the other species can move their rhinophoral sheaths. The sheaths take the form of semicircular flanges in *T. pennigera* (Montagu), *T. pacifica* Bergh, and *T. darwini* Pruvot-fol. They are triangular in *T. picta* Baba and the new species from South Africa figured by Gosliner (1987a, number 170); in that latter species there is also a papilla arising from the anterior angle. The recurved anterior margin and high pointed posterior corner of the sheath of *T. boyla* suggest greatest similarity with that of *T. picta*. In having a pattern of coloured spots, *T. boyla* resembles *T. pennigera* and *T. darwini*. In *T. pennigera*, however, the spots are larger and orange or black (see: Brown & Picton, 1979, p. 16; Willan & Coleman, 1984, number 24; Thompson & Brown, 1984, plate 19d and 19e; Gosliner, 1987a, number 168). Unfortunately the coloration of *T. darwini* is insufficiently described (Er. Marcus, 1959, p. 57) to enable any comparison with that of *T. boyla*. The extra-branchial processes of *T. boyla* are not conical and ceratiform as is typical of the genus; instead they are bulky, flattened and triangular. *T. boyla* has a relatively shorter tail than *T. pennigera*. *T. boyla* has, as an adult, the smallest number of gills of any species; *T. pennigera*, *T. pacifica* and *T. darwini* have 5, and *T. picta* has seven. The radular formula, tooth shape and wing-like form of the jaws are perfectly typical of the genus. The trialectic reproductive system is similar to that of *T. darwini* (see Er. Marcus, 1959) and *T. pennigera* (see Willan, 1976); in all three species the ampulla is kidney-shaped, the bursa copulatrix is spherical, the prostate gland is enlarged and ensheaths the spherical bursa, the distal vas deferens is long and the penis is spinose. In *T. darwini* an accessory sperm sac is present as a distinct vesicle at the of the receptaculum seminis. In *T. pennigera* the distal vas deferens is relatively shorter and the receptaculum seminis arises relatively further away from the bursal stalk.

DISCUSSION OF THE GENUS *Thecacera*

The discovery of the new species of *Thecacera* described herein prompted a review of the genus as a whole. The unique rhinophoral "tentacles" of *T. boyla* necessitate a slight broadening of the pre-existing generic definition (Willan, 1976, p. 351) to cover all types of sheath - i.e., from a semicircular flange to triangular to triangular with anterior papilla, to enlarged tentaculate - and recognition that in one species at least, sheaths of the enlarged "tentaculate" kind are highly mobile. As

reported above, my observations suggest this mobility is related to sensory input rather than defense. I suggest that these "tentacles" are analogous in function to the velar papillae of the sister genus *Polycera*. However, all the other characters of *T. boyla* are so typical of *Thecacera* we can conclude unequivocally that the genus is a natural (i.e., holophyletic) one. As I will expand on the genus' autapomorphies in the following section it is unnecessary to list them here.

Thecacera is a small genus. In the author's previous review (Willan, 1976), six species were listed: *T. capitata* Alder & Hancock; *T. darwini*; *T. pacifica*; *T. pennigera*; *T. picta*; *T. virescens* Alder & Hancock. Subsequent re-examination of the type material of *T. capitata* has shown that species to be a synonym of *Polycera quadrilineata* (Müller) (Turk, 1981, p. 296; Thompson & Brown, 1984, p. 71; Thompson, 1988). Furthermore, Thompson (1988) states that *T. virescens* is "probably" a synonym of *Polycera nothus* (Johnston). *T. boyla* plus the undescribed South African species (Gosliner, 1987a, number 170) bring the total back up to six.

PHYLOGENETICS

The phylogenetics of the family Polyceridae (which I regard as distinct from the Triphoridae) will make a fascinating future study, particularly in an Hennigian context. *Thecacera* possesses a suite of apomorphies; they are: absence of oral tentacles; propodial tentacles; pre-rhinophoral pits; rhinophoral sheaths (reaching their zenith in *T. boyla*); reduction of gill number; extra-branchial processes; integumentary spicules; wing-like jaw form; absence of rachidian row of radular teeth; vas deferens with enlarged central prostatic section that ensheaths bursa copulatrix; armed penis. The last three of these characters are synapomorphous with *Polycera* and both genera have identical radular architecture. These observations support the accepted view that *Thecacera* is closer to *Polycera* than any other polycerid genus (i.e., *Polycerella*, *Issena*, *Nembrotha*, *Roboastra* or *Tambja*). However, *Thecacera* shares synapomorphies with at least two of these genera. Burn (1978) described pre-rhinophoral pits in a species of *Tambja*. Post-branchial processes, or their precursor/derivative tubercles, are always present in *Polycerella* and most species of *Polycera*. Perhaps these two character states are, in reality, autapomorphies for the Polyceridae like the projection on the shaft of the lateral radular teeth? Although I am wary of using food in a phylogenetic context, I note *Thecacera* and *Polycera* do share the same bryozoan diet - even the same genus of bryozoan (*Bugula*) - with *Tambja* and some species of *Roboastra*. In overview, it would appear that *Thecacera* was derived from a *Polycera*-like polycerid and it has subsequently elaborated the anterior foot margins into propodial tentacles, anterior notal brim into rhinophoral sheaths, and developed pedicel spicules.

ZOOGEOGRAPHY

Because all the specimens of *Thecacera boyla* have been taken from the immediate vicinity of Townsville in northern Queensland, they are insufficient to tell us anything of the species' range. However this species' occurrence provides one more piece in the biogeographical jigsaw puzzle that is this genus' distribution. Having established that *Thecacera* is holophyletic, the exercise of solving that particular puzzle becomes worthwhile. *T. boyla* is the fourth species with a primarily tropical distribution, the others being *T. picta*, *T. pacifica* and the new South African species (Gosliner, 1987a, number 170). Because *T. pennigera* has

also been recorded from tropical locations like Pakistan (Eliot, 1905), the Red Sea (Eliot, 1908), Ghana (Edmunds, 1977) and Mauritania in northwestern Africa (Dekker, 1986), it might actually have originated in the tropics. I do not wish to imply I presently hold this view, just that it is a possibility. But if it is true, then 83% of species of *Thecacera* will be tropical and the conclusion inescapable that *Thecacera* is tropically centered.

Thecacera pennigera is biogeographically the most problematic species in the genus. Presently it has an almost cosmopolitan range (summarized by Willan, 1976). Since my summary, Edmunds (1977) reported a population in Ghana, and other recent papers have reinforced the known range (Burn, 1978; Dekker, 1986; Gosliner, 1987a,b). Taken together, these new records confirm this species has not only a wide thermal tolerance but is also capable of reproducing in temperate waters. I hypothesized that this present day distribution of *T. pennigera* was not natural but the result of distribution by shipping as part of the fouling community on boats' hulls (Willan, 1976). Gosliner (1987b) queried this shipping hypothesis in the case of South Africa where he found specimens on the open coast several hundred kilometres from the nearest harbour. He suggested that some factor other than accidental human transportation was responsible for the occurrences he observed. This other factor might be larval transport, but it might be that (tropical) southeastern Africa was indeed the original home of *T. pennigera*. It is unlikely that this species' original range will ever be known with certainty (Willan, 1976).

Setting *T. pennigera* aside, there are apparently two wide-ranging and three relatively short-ranging species of *Thecacera*. *T. pacifica* occurs in the Red Sea as well as throughout the tropical Indian Ocean east to the Arafura Sea, but despite its specific name it is unknown from the Pacific Ocean. Specimens of *T. picta* collected at Malakal channel, Palau Islands, by Mr C. Carlson in July 1969 and at Cartier Island, west of Ashmore Reef, Timor Sea, by Dr F.E. Wells in September 1986 (one at each locality) indicate that species is probably widespread in tropical waters between Australia and Japan. *T. darwini* is known from southern Chile (Pruvot-Fol, 1950; Er. Marcus, 1959). The new South African species is known from Sodwana Bay to Umgazana (Gosliner, 1987a). *T. boyla* is presently localized from coastal northern Queensland. Although it is difficult to deduce any zoogeographical pattern for the genus, there appears to be greatest species diversity in tropical southeastern African waters and progressive impoverishment eastwards from there.

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